RESEARCH ARTICLE

Modelling the invasion dynamics of the African citrus psyllid: The role of human-mediated dispersal and urban and peri-urban citrus trees

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Abstract

The African citrus psyllid, *Trioza erytreae* (Del Guercio) (Hemiptera, Triozidae), is native to tropical Africa and invasive species in North America and Europe. The main host plants are citrus, displaying a preference for lemon trees. This psyllid was recently detected in the northwest region of the Iberian Peninsula, both in Spain and Portugal. Here, we used a model combining a reaction-diffusion model to a stochastic long-distance dispersal model to simulate the invasion dynamics of *T. erytreae* in Portugal. The psyllid spread in Portugal was simulated between 2015 and 2021 for different combinations of model parameters: two fecundity levels; spread with and without stochastic long-distance dispersal; single or two introductions of *T. erytreae*; and considering or not the urban and peri-urban citrus trees, besides citrus orchards, estimated using Google Street view imagery. The incorporation of long-distance human mediated dispersal significantly improved the F1-score in the model validation using the official reports as the observed data. Concomitantly, the dispersal rate of *T. erytreae* in Portugal was on average about 66 km/year, whereas removing long-distance dispersal events, the observed mean was 7.8 ± 0.3 km/year. The dispersal was mainly towards the south along the coastline, where human population is concentrated. The inclusion of the estimated citrus trees outside orchards areas significantly increased the F1-score in the model validation, revealing the importance these isolated host plants hold as stepping stones for the species current invasion and possibly for other species alike.

Keywords

Introduction

Pest species introductions outside the native range have significantly increased in the last decades worldwide (Walther et al. 2009; Seebens et al. 2017; Turner et al. 2021). This is mainly attributed to the intensification of global trade and human travel (Roques 2010; Brockerhoff and Liebhold 2017). Some of these introduced species are invasive, causing high ecological and/or economic impact in agricultural or forest ecosystems (Pimentel et al. 2005; Kenis et al. 2009; Zenni et al. 2021).

The African citrus psyllid, *Trioza erytreae* (Del Guercio) (Hemiptera, Triozidae), is a small sap-sucking insect, native to tropical Africa (Moran and Blowers 1967). The main host plants of *T. erytreae* are Rutaceae, such as citrus, displaying a preference for lemon trees (*Citrus limon*) over sweet orange trees (*Citrus sinensis*) (Aubert 1987). The psyllid was recently introduced in Continental Europe. It was detected in the northwest region of the Iberian Peninsula, both in Spain in 2014 and in Portugal in 2015 (Monzó et al. 2015; Pérez-Otero et al. 2015; DGAV 2021). The introduction of this invasive species has drawn major attention, as it is a vector of the huanglongbing (HLB), also known as the greening disease (McClean and Oberholzer 1965), considered the most damaging citrus disease in the world. The disease is caused by the *Candidatus liberibacter* spp. bacteria (Bové 2006; Gottwald 2010), which is not yet present in Europe. Illustratively, since HLB was introduced in Florida, orange production dropped by 74%, between 2005 and 2019 (Singerman and Rogers 2020). In Europe, *T. erytreae* and HLB are classified as A2 (Annex II B) and A1 quarantine pests (Annex II A), respectively (EU 2019; EPPO 2022a; 2022b).

Since its detection, *T. erytreae* has been expanding southwards along the Portuguese coastal area, despite the phytosanitary measures that were implemented by the Ministry of Agriculture to contain its spread (DGAV 2021). It has a high invasive potential due to its high fecundity (between 327 and 827 eggs per female), no diapause and multivoltine biological cycle (up to 8 generations per year) (Moran and Blowers 1967; Catling 1969, 1972; Tamesse and Messi 2004). However, the number of yearly generations can be reduced to three in hot and dry summer conditions or other unfavourable conditions for the host leaf flushing, as *T. erytreae* reproduction requires the availability of young leaf shoots (Catling 1972; Tamesse and Messi 2004; Cocuzza et al. 2017). Adults of *T. erytreae* were estimated to fly up to 1.5 km, especially if forced by external factors, such as lack of leaf flushes (Samways and Manicom 1983; Van den Berg and Deacon 1988). Its dispersal may be further aided by wind currents, as was shown in the case of the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Aubert and Hua 1990; Antolínez et al. 2022. Human activities, such as the transportation of fruit or plant material, may also be involved in the long-range dispersal of the species (Aubert and Hua 1990; Antolínez et al. 2022. This has been shown for other agricultural and forest pests (Shigesada and Kawasaki 1997; Tobin and Blackburn 2008; Robinet et al. 2009), including the Asian citrus psyllid (Halbert et al. 2010).

Citrus orchards in Portugal represent around 19,000 ha, mostly concentrated in the south of the country, the major production region (EU 2021). However, besides

citrus orchards, it is common to find citrus plants in urban and peri-urban landscapes, all over the country, including urban trees in villages and cities, mostly in central and southern Portugal, but also trees in home gardens and backyards (Duarte 2012). These citrus trees are not included in the official statistics and may represent a significant area within the global spatial distribution range of citrus plants in Portugal, which has not been estimated. They may have an important role in the dispersal of *T. erytreae*. Indeed, scattered host plants could play an important role in the spread of invasive species, in general, as was clearly demonstrated for the pine processionary moth, *Thaumetopoea pityocampa* Denis & Schiffermüller (Rossi et al. 2016). For *T. erytreae*, isolated citrus trees may be a reservoir of the psyllid (Van den Berg et al. 1991) and they are expected to influence the connectivity between the fragmented citrus producing lands.

A few studies used the bioclimatic suitability of the different geographic regions of Portugal and Spain to predict the potential spread of *T. erytreae* (Benhadi-Marín et al. 2020, 2022; Paiva et al. 2020). Paiva et al. (2020) used the water vapour pressure deficit (based on the results of Green and Catling 1971) to predict climate suitability for the psyllid, in Portugal, based on data collected from 18 weather stations, distributed throughout the country. Benhadi-Marín et al. (2020) carried out a pest risk analysis modelling approach to predict the expected spread of *T. erytreae* in the Iberian Peninsula. They compared three models: (1) a radial range expansion model, (2) a hybrid model of logistic growth and radial rate and (3) the deterministic version of the dispersal kernel model. The kernel model with two hypothetical entry points (Vila Nova de Arousa, in Spain and Porto, in Portugal) showed to accurately predict the distribution of the psyllid with respect to latitude, five years after its detection. More recently, the same research team refined the approach used previously (Benhadi-Marín et al. 2022) by: improving the spatial data resolution (1 km); including a physical barrier (altitude of 400 m) and long-distance dispersal events (cells up to 500 km apart were allowed to be colonised) for modelling purposes; extending the prediction to 30 years after the introduction of *T. erytreae* in the Iberian Peninsula; simulating different scenarios (very low, low, medium and high spread). Using this approach, Benhadi-Marín et al. (2022) identified three key risk areas, one in Portugal, the citrus growing areas of Setúbal and two in Spain, Huelva and the potential citrus corridor that connects Guipúzcoa, claiming that these areas should have special attention for the monitoring of *T. erytreae*.

To explore the role of human activities in the spread of *T. erytreae* in continental Portugal, we used a model that combined a reaction-diffusion model to simulate the natural spread of the species and a stochastic long-distance dispersal model to simulate human-mediated dispersal of the species. Reaction-diffusion models have been commonly used for simulating the spatial spread of invasive species as they describe both population growth and population dispersal in a spatially explicit way to provide an estimate of population density over time and space (e.g. Shigesada and Kawasaki 1997). These models describe diffusive dispersal (e.g. dispersal into adjacent habitats), but cannot describe jumps at long distances. To model explicitly a stratified dispersal (allowing both diffusive dispersal and long-distance jumps), we thus combined a reaction-diffusion model to a stochastic long distance dispersal model. This approach has been previously used to explore the role of

human mediated dispersal in expanding insect populations (e.g. Robinet et al. 2019). To our knowledge, this is the first time this modelling approach is used for *T. erytreae*. Our specific objectives were: (i) to understand the role that human-mediated spread has played in the current invasion of the psyllid in Portugal; (ii) to highlight the importance of trees outside citrus orchards in the psyllid's spread and the general importance that isolated trees data can have for large-scale pest species modelling. With this aim, we provided an important innovation in the utilisation of Google Street view imagery to estimate citrus trees density in urban and peri-urban areas. Finally, we tested the hypothesis of multiple introductions of *T. erytreae*, as suggested by Ruíz-Rivero et al. (2021).

Materials and methods

Model development

A reaction-diffusion model was developed to simulate the local spread of *T. erytreae* since its arrival in Portugal for the whole continental area of the country. This type of modelling is commonly used for describing the spatial spread of invasive species (e.g. Shigesada and Kawasaki 1997). The model which incorporates the dispersal of the species and the population's growth can be expressed using the following Fisher equation:

$$\frac{\partial N}{\partial t} = D\left(\frac{\partial^2 N}{\partial x^2}+\frac{\partial^2 N}{\partial y^2}\right) + rN\left(1-\frac{N}{K}\right) \qquad \text{eq.1}$$

where N is the population density of *T. erytreae* (km^{-2}), dependent on time t and spatial location (x,y); D is the coefficient of diffusion (km^2 /year); r is the population growth rate (year^{-1}); and K is the carrying capacity (km^{-2}). The model exhibits a travelling wave with a constant spread rate (C; km/ year) defined by:

$$C = 2\sqrt{rD} \qquad \text{eq.2}$$

where C, K and r were all estimated beforehand (see text below), while D was assumed to be homogeneous across Portugal, based on eq. 2 (similarly to Robinet et al. 2017), considering C and r of the area infested by *T. erytreae* at the end of 2015.

The model described was applied over a grid of 5 km × 5 km resolution, from 2015 to 2021 with a yearly time step.

The population dynamics and spread parameters were obtained, based on previous research studies on the biology and ecology of the psyllid, so that model simulation could be then validated using the independent presence/absence of observed data.

Spread rate and carrying capacity

The estimate of the local spread rate C (6 km/year) was based on the maximum flight capacity of *T. erytreae* determined by Van den Berg and Deacon (1988), i.e. 1.5 km,

multiplied by 4, the estimated number of yearly generations that *T. erytreae* can have in Porto, where *T. erytreae* was first detected.

The carrying capacity K was estimated for each cell in the model, as the product of the average maximum capacity of *T. erytreae* per host tree, k_{tree} and the estimated number of citrus trees in the cell. k_{tree} was determined using data from Catling (1972), corresponding to the mean number of individuals per citrus tree (adults, nymphs and eggs), observed in a 3-year study, under favourable conditions, using the following formula:

$$k_{tree} = \text{Adults} + (0.289 \times \text{Nymphs} + (0.289 \times 0.95 \times \text{Eggs}) \qquad \text{eq. 3}$$

where 0.289 is the nymphal survival rate under natural conditions (Caitling 1970) and 0.95 is the egg viability in optimum environmental conditions (Catling 1972; Van den Berg et al. 1991) to obtain k_{tree} = 2719 adults of *T. erytreae* per tree.

To estimate the spatial density of citrus trees in orchards throughout the country, we used the data from the 2019 agricultural census (INE 2021). This dataset does not include citrus plants in urban and peri-urban areas, as well as isolated citrus trees in rural landscapes. The dataset from INE (2021) provides the area of citrus orchards per county. The density of citrus trees in orchards was assumed, for simplicity, to be the same all over the territory, i.e. 400 citrus trees/ha, considering 5 m × 5 m per tree. Although citrus-tree spacing may vary between 5 m × 4 m or lower and 7 m × 5 m (Cavaco and Calouro 2005; Vacante and Gerson 2012), we considered for simplicity a median value of 5 m × 5 m. The citrus tree density for each 25 km² grid cell of the model was estimated, based on spatial data from the Land Use and Occupancy Mapping - COS2018, (available at https://www.dgterritorio.gov.pt/) and the data from the 2019 agriculture census (INE 2021), about the area of citrus orchards.

As data on the density of citrus trees in urban and peri-urban areas were not available from the 2019 agriculture census (INE 2021) and considering its possible influence on the dispersal of *T. erytreae*, we developed an innovative approach to estimate it. We used the spatial data of the COS2018 dataset, to classify the urban and peri-urban areas. Then, we divided these areas into three different classes: Vertical urban areas; Horizontal urban areas; and Discontinuous urban areas (see S1). For each class, the mean density of citrus trees was estimated using Google Street view imagery to survey the number of visible trees in randomly selected polygon areas extracted from the COS2018 spatial dataset throughout the country (Rousselet et al. 2013; Berland and Lange 2017). The estimations were made using the survey counts of citrus trees in each area, weighted against the sample area sizes. Only areas with good image quality were used. We surveyed at least 250 ha for each of the three urban classes considered to provide a confident estimation of citrus tree density. All the surveys were conducted by the first author.

Growth rate

To calculate the growth rate, r, for *T. erytreae* in Portugal, we used climatic modelled data collected for 30 years (Palma 2017). These data were collected for each centroid

of a grid of 25 km × 25 km covering Portugal. The climatic variables considered were the daily mean temperature, daily maximum temperature and the daily minimum relative air humidity. The average daily climatic data were grouped into three periods per month. Each period had 10 days, except the last third of each month, which varied from 8 to 11 days, depending on the month. These periods are henceforth called as "10-day periods", needed to calculate the *T. erytreae* survival rate, using the method developed by Catling (1969).

For each 10-day periods, the number of "viable days" (i.e. the number of days above the lower temperature threshold for development) was calculated. Temperatures were estimated, based on the average of the 30 years of the climatic data. A lower temperature threshold of 12.0 °C was considered, based on citrus tree growth not occurring below these temperature values (Webber and Batchelor 1943; Kumar 1977), as well as the inability of *T. erytreae* larva growth (Catling 1973). An upper temperature threshold was not used since we took into consideration the effect of high temperature and low humidity in the variable weather survival.

Weather Survival (*WS%*) was calculated for each 10-day period, using the mean Vapour Pressure Deficit (*VPD*) of the three days with the highest daily values of maximum temperature, using Saturated Vapour Pressure (*SVP*) (Murray 1967; Green and Catling 1971):

$$VPD = ((100 - RH)/100) \times SVP \qquad\qquad \text{eq. 4}$$

$$SVP = 610.7 \times 10^{7.5\,Tmax/(237.3+Tmax)} \qquad\qquad \text{eq. 5}$$

$$\text{Weather Survival } (WS\%) = 0.0308\, X_3^2 - 4.1825\, X_3 + 137.7709 \qquad \text{eq. 6}$$

where X_3 is the mean value of the *VPD* in millibars, of the three days with the highest maximum temperatures during the 10-day period.

For the model calculations, we used Weather Mortality (*WM%*):

$$WM = 1-(WS/100) \qquad\qquad \text{eq. 7}$$

For each area, the number of possible yearly generations was then estimated, as the sum of life cycle progress rounded down from each yearly 10-day period from February until the end of September, the most important period of leaf flushing for citrus trees in Portugal (Paiva et al. 2020). Life Cycle Progress was calculated by dividing the average viable days and the estimated total life cycle duration in days for each 10-day period, calculated using the average temperature of the viable days (*VD*) and the life cycle duration (*G*), that is the expected total number of days to successfully complete the insect life cycle from egg to adult.

$$\text{Life Cycle Progress} = VD / G \qquad\qquad \text{eq. 8}$$

The life cycle duration G, in days, was calculated, based on the number of days needed to complete egg incubation (*Idays*) plus the number of days needed to complete nymphal growth (*Ndays*), based on the equations proposed by Catling (1969). To this period, we added 5 days of the pre-oviposition period, being the mean of the pre-oviposition time of the species (Van der Merwe 1923; Catling 1973; Van den Berg 1990) and another 10 days to reach the peak of oviposition (Catling 1973).

$$Idays = 4.9763 + 3.3443 \times 0.8452^{\text{Tmed-20}} \qquad \text{eq. 9}$$

$$Ndays = 16.7974 + 5.2726 \times 0.7843^{\text{Tmed-20}} \qquad \text{eq. 10}$$

$$G = Idays + Ndays + 15 \qquad \text{eq. 11}$$

The growth rate at a given time period t in the year, R_t was calculated as:

$$R_t = f \times 0.5 \times (1-WM) \times (1-0.8\ WM) \times (1-0.3\ WM) \times$$
$$(1-0.15\ WM) \times (1-0.075\ WM) \times 0.289 \qquad \text{eq. 12}$$

where f is the female fecundity, estimated by the average number of eggs per female. Due to the different fecundity estimates reported in literature, we tested two different values, i.e. 827 and 327 eggs per female (Moran and Blowers 1967; Catling 1969) in the model. The mean fecundity value was multiplied by egg viability rate, estimated as 0.95 in optimal environmental conditions (Catling 1972). We assumed a sex ratio of 1:1 (Van den Berg 1990). WM, $0.8\ WM$, $0.3\ WM$, $0.15\ WM$, $0.075\ WM$ correspond to the weather mortality for the 1st, 2nd, 3rd, 4th and 5th instars, respectively, since larval stages increasingly become more resilient to the adverse environmental conditions (Catling 1972). Finally, 0.289 is the natural survival rate from egg to adult in "perfect conditions", with the presence of natural enemies, according to Catling (1970).

For the remaining generations, we considered a geometric growth, $N_t = N_{t-1} R_t$

The resulting $R^G =, \prod R_t$ where G is the maximum potential generations in each cell per year, will reflect the total growth potential of the species in the area for one year (Pointeau et al. 2021). The intrinsic yearly growth rate of the cell is then calculated as follows:

$$r = \ln(R^G)$$

We repeated this procedure for each cell of the model.

A cold limitation factor was further generated considering the reproduction of this species is limited by extremely cold temperatures. Cold and long winter periods can hinder population reproduction and limit the species' capacity to stay in the region throughout the entire year. Thus, we consider that regions having on average less than 2 days of viable days (i.e. with a mean daily temperature

above 12.0 °C), for the three consecutive winter months (December, January and February), were not suitable for *T. erytreae* to establish. The model found that, in these areas, the number of *T. erytreae* was always 0. The period of three months is based on the maximum longevity of 82 days recorded for the species during winter (Catling 1969).

Long distance dispersal

Modelling long-distance dispersal is always very challenging since it is based on stochastic and relatively rare dispersal events. To model human-mediated long-distance dispersal, we calculated the number of long-distance dispersal events (*NB*) that occur in each year, which was randomly chosen using the following equation:

$$NB = 1 + e \qquad\qquad \text{eq. 13}$$

where *e* denotes an independent and identically distributed random variable with a Poisson distribution with mean $\lambda = (\ln((P/2642)+1/\ln(2)) \times 5)$, with *P* being the number of cells estimated to be infested at a given time *t* and 2642 is the total number of cells that can be infested in the model.

   We used the Poisson distribution as it is a simple discrete distribution that is often used to model jump processes (Hooten and Wikle 2008). The mean λ was defined as a concave increasing function of *P*, with a minimum value of 2.8 when *P* = 0 and a maximum value of 6.0 when *P* = 2642. In this way, the number of simulated long-distance jumps increases with the area infested, taking relatively realistic values compared to the spread pattern observed.

   For parameter testing, we made simulations using low-frequency jumps, with low λ = (mean λ)/2 and high frequency jumps with high λ = (mean λ) x 2.

   For each long-distance dispersal event, the model randomly chooses a cell that is not yet infested (*N* < 1), with a growth rate r > 1 and a suitable human population density. The minimum human density threshold (*H*) allowing the arrival of a long-distance jump was set to 125 habitats/km², using the same threshold considered for the spread of the yellow-legged wasp in France (Robinet et al. 2017), which also delimits urban areas relatively well in Portugal, being mostly in the coastal areas of the country, represented as dark red areas in Fig. 1. A recent study showed that both the distance to roads and urbanisation intensity play an important role in spatial and temporal dynamics of the dispersal of the Asian citrus psyllid, *D. citri* in California (Bayles et al. 2022). We did not use road network data nor urbanisation intensity due to lack of reliable complete data available for Portugal. Instead, we used human population density (data from 2017 available at https://www.ine.pt/), as it was demonstrated to being a suitable proxy for road traffic in Portugal (Barata 2012).

   Cells infested by such long-distance jumps received an arbitrary set of 50 individuals.
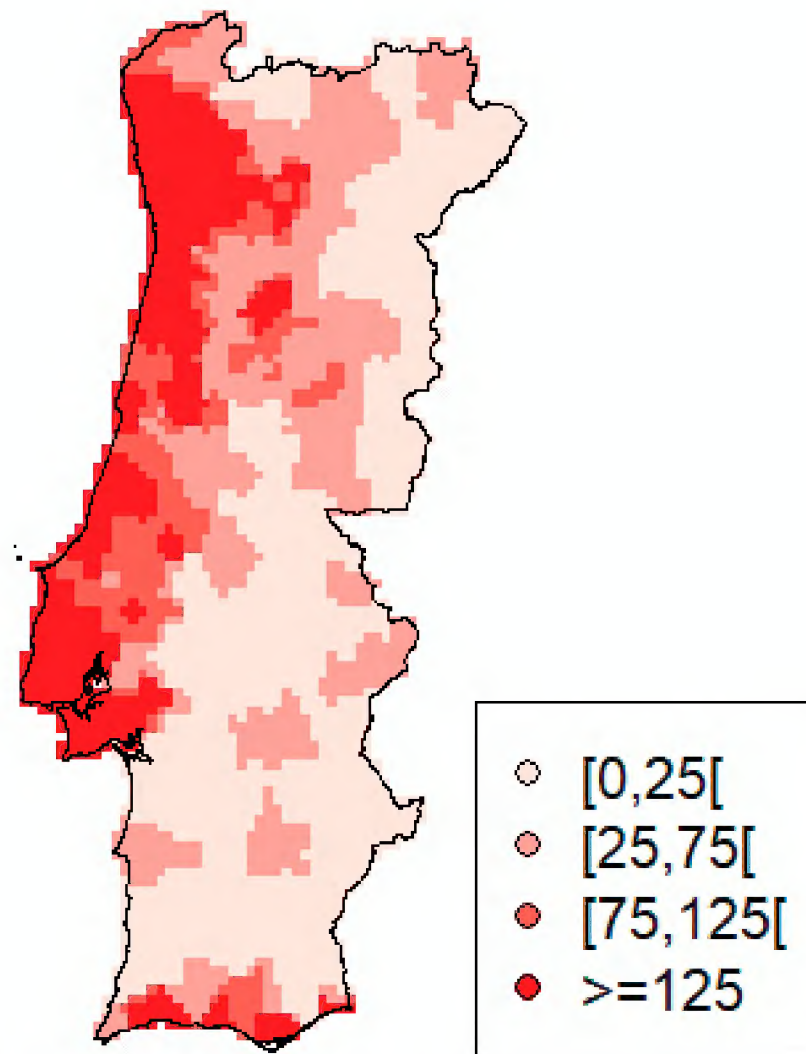
Figure 1. Distribution of the human population density in Portugal (number of inhabitants/km²) in 2017. The human population threshold of 125 habitants/km² was used to characterise locations where long-range distance dispersal could occur in the model.

Multiple introductions

A molecular study on the genetic diversity of *T. erytreae* populations in the Iberian Peninsula suggested the possibility of multiple introductions of the psyllid (Ruíz-Rivero et al. 2021). Two main genetic clusters were observed along the Portuguese coast. Based on these results, we defined two possible scenarios in the model: 1) one single introduction of *T. erytreae* in the north (Porto in 2014); 2) two introductions, the first in the north (Porto in 2014), and a second in the region of Lisbon (Lisbon in 2017), which has an international port and airport. For the second introduction scenario, we added 1000 individuals to a specific cell in the Lisbon area, where *T. erytreae* was first detected in the region (data provided by the Portuguese National Plant Protection Authority reports).

Model running and validation

We combined estimates of local spread and growth with estimates of long-distance dispersal. We applied these models on a grid that covers Portugal with a spatial resolution

of 5 km × 5 km. The simulation began in 2014 in one cell in the Porto region with 1000 individuals for the initial condition of the invasion, which was later discovered already spreading, in 2015.

Since the first detection of *T. erytreae* in Porto, in 2015, the Portuguese National Plant Protection Authority, has been monitoring the species spread at the parish level, with the deployment of a trapping protocol surrounding the infested areas within a 3 km buffer range, with yellow-sticky traps and additional, monitoring within 10 km range. In addition, they also included reports from citizens and stakeholders, after confirming their authenticity. Reports are publicly available whenever there are newly-infested areas (available at: https://www.dgav.pt/plantas/conteudo/sanidade-vegetal/inspecao-fitossanitaria/informacao-fitossanitaria/trioza-erytreae/). This complete data-set was provided to us by the Portuguese National Plant Protection Authority (DGAV). We compiled it yearly and used it to validate our model, as well as determining the dispersal capacity, from 2015 until the end of 2021. All the parameters used for the model were estimated independently from this presence/absence observed data, allowing for independent validation.

To validate the model and identify the dispersal scenarios that best fit the observed data, the species' spread was simulated between 2014 and 2021 for different combinations of model parameters (Table 1).

For the simulations considering long-distance dispersal (stochastic sub-model), we ran 300 replicate simulations using randomly generated long-distance events.

We consider that a cell is infested when N ≥ 1 individual.

For the replication of simulations considering long-distance dispersal, we calculated the percentage of simulations that classified each cell as infested. For each cell, if 50% or more simulations predicted the infestation, then the model classifies those cells as infested. Thereafter, for each model, using the simulation data from 2021, we calculated the *F*1-Score performance criteria (Chinchor and Sundheim 1993), using the following equation:

$$F1-\text{Score} = \frac{2x(\text{ precision } x \text{ recall })}{\text{precision } + \text{ recall}} = \left(\frac{TP}{TP + \frac{1}{2}(FP + FN)} \right) \qquad \text{eq.14}$$

where *TP* is the sum of true positives, *FP* is the sum of false positives and *FN* is the sum of false negatives. *F*1-score is the harmonic average of precision and recall.

We compared models with different parameters using the model's performance criteria, *F*1-Score. We also calculated standard errors for each model's *F*1-Score, using 2000 bootstrap simulations taken from the 300 original simulations of each stochastic model. These were used to obtain the *p*-values for testing the equality of the *F*1-Score for pairwise comparisons between two models. *P*-value was calculated by the inversion of the bootstrap normal confidence interval for the difference in means (Thulin 2021) using the following equation:

$$P\text{-value} = 2\left(1-2\left(1-\Phi^{-1}(F1a-F1b)/(\sqrt{SEa+SEb}\right.\right. \qquad \text{eq.15}$$

where Φ^{-1} denotes the inverse cumulative distribution function of the standardised normal distribution. $F1a$ and $F1b$ are the $F1$-score of model a and model b, respectively and SEa and SEb are the Standard error values of model a and model b, respectively.

We also calculated the Area Under Cover (AUC) of the receiver operating characteristics plots (Fielding and Bell 1997) and the Youden index of each model (Youden 1950), but they led to the same conclusions as $F1$-Score.

The tested parameters were the two different female fecundity rate values (Low or High), the inclusion or not of long-distance dispersal events (Yes or No), the frequency of the long-distance dispersal events (Low, Medium, High), the inclusion of the estimated residential urban citrus trees (Yes or No) and the occurrence of a second introduction of *T. erytreae* in Lisbon (Yes or No) (Table 1).

We compared the estimated local spread rate value against the observed short-range dispersal, based on presence-absence data reports from DGAV. For each year, we calculated the mean least distance between all newly-infested parishes centroids and past infested parish centroids (*DP*). Infested parishes attributed to long-distance dispersal were removed from the short-range dispersal rate calculation. We identified such parishes, when their *DP* was higher than 30 km or was higher than the distance between its centroid and a long-distance dispersal parish centroid. Thirty km is an arbitrary distance value that is significantly higher than the yearly estimated flight capacity of *T. erytreae* and three times the 10 km radius used by the Portuguese Plant Protection Authority for the species monitoring. Finally, with the average value of *DP* from each year, we calculated the average short-range dispersal rate of *T. erytreae* in Portugal for each year and in total using all *DP* values independently of the year of infestation. Furthermore, to calculate the total dispersal capacity to the east and to the south of the country, the main directions the species could spread in Portugal, we used the distance between the infestation origin and the furthest parish towards the east and the south,

Table 1. Parameters and scenarios tested in the modelling.

Model parameters	Scenarios tested	Details
Long-distance dispersal (LDD)	No, Low,	No = No LDD
	Medium, High	Low = λ = (log((*P*/2642)+1/log(2)) × 5) / 2
		Medium = λ = (log((*P*/2642)+1/log(2)) × 5)
		High = λ = (log((*P*/2642)+1/log(2)) × 5) × 2
Fecundity	Low, High	Low = 327 eggs/female
(Fecund)		High = 827 eggs/female
Number of introductions of *T. erytreae*	True	True = Two introductions; in Porto 2014 and Lisbon 2017
(LIS)	False	False = One introduction in Porto
Host trees available	True	True = Trees from orchards, plus trees from urban and peri-urban areas
(Urb)	False	False = Trees from orchards only

as was done for the spread pattern of *V. velutina* (Verdasca et al. 2021). Additionally, we calculated the total infestation area of the infested parishes along the invasion years.

Model simulation running, validation and all statistical analysis were done with the statistical language R version 4.2.0 (R Core Team 2022). Modelling Data and R code are available at https://zenodo.org/record/7096566.

Data resources

Portuguese National Plant Protection Authority (DGAV) *Trioza eytreae* Reports – Available at https://www.dgav.pt/plantas/conteudo/sanidade-vegetal/inspecao-fitossanitaria/informacao-fitossanitaria/trioza-erytreae/. Cos2018, Land Use and Occupancy Map 2018 – Available at https://www.dgterritorio.gov.pt/. Agricultural census of 2019 (INE 2021) - Available at https://www.ine.pt/xurl/pub/437178558. Human population density in Portugal from 2017 – Available at https://www.ine.pt/. The R script and the data needed to run the model - Available at https://zenodo.org/record/7096566.

Results

Spread rate

The reports of the Portuguese Plant Protection Authority denote a fast dispersal of *T. erytreae* in Portugal (Fig. 2). Between 2015 and 2021, the African citrus psyllid was able to spread mostly southwards, along the coastal area of Portugal, covering a maximum distance of about 461 km, between Porto and western Algarve and a cumulative area of about 14,239 km² (Fig. 2). This corresponds to an average of about 65.9 km/year and 2034 km²/year. The dispersal towards the east was only 100 km (14 km/year). However, removing long-distance dispersal events, the observed mean dispersal rate of *T. erytreae* in Portugal was 7.8 ± 0.3 km/year (Table 2). The estimated short-range dispersal capacity used in our model simulation was 6 km/year, which turned out to be very close to the observed data (ranging from 5.6 to 10.4 km/year) (Table 2).

Growth rate

Our estimates of the number of yearly *T. erytreae* generations in Portugal varied from 3 to 4 generations per year. The estimated grow rate (*r*) of *T. erytreae* in the Portuguese territory was found to be higher along the coast area (Fig. 3). A different female fecundity rate had a major impact on the growth rates estimated, especially in the interior central and southern regions (Fig. 3). The model included a cold limiting factor, portraying areas whose winter was deemed as too extreme for *T. erytreae* survival, where the growth rate was 0. The cold limited areas are all located in the northern interior part of the country (Fig. 3), where most areas are mountainous and the climate is colder, especially in the winter.
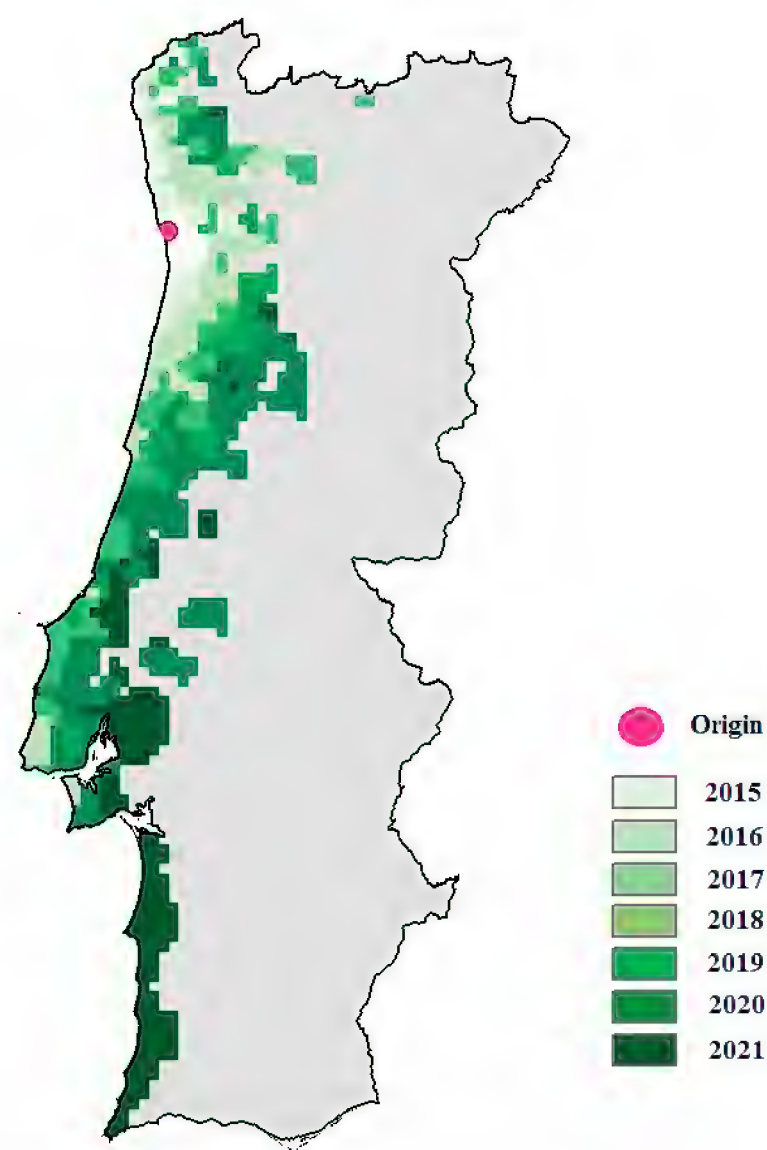
Figure 2. Spatio-temporal representation of Portugal's invasion by *Trioza erytreae*, between 2015 and 2021. Elaborated, based on data from the published by the Portuguese Plant Protection Authority.

Table 2. Short-range yearly mean dispersal distance (± SE) and area of *Trioza erytreae* in Portugal, between 2015 and 2021, based on the reports published by the Portuguese Plant Protection Authority.

Short-range dispersal rate	2015	2016	2017	2018	2019	2020	2021	Total
Mean dispersal distance (km)	10.4 ± 1.3	7.5 ± 2.8	8.5 ± 0.8	5.6 ± 0.6	7.9 ± 0.7	8.1 ± 0.6	5.6 ± 0.6	7.8 ± 0.3
Dispersal area (km²)	384.7	698.4	1604.5	1612.0	1075.2	4401.7	4462.0	2034.1

Host availability

According to the most recent agriculture census of Portugal, there is a total surface of 21,681 ha of citrus orchards in continental Portugal, 74% of which located in the south, in the Algarve Region (INE 2021). We estimated a total of 11,993,645 citrus trees in orchards and 7,427 trees in urban and peri-urban areas (Fig. 4). The estimated citrus-trees density in Vertical, Horizontal and Discontinuous urban areas were 0.37, 3.2 and 5.14 trees per hectare, respectively (see Suppl. material 1: table S1).
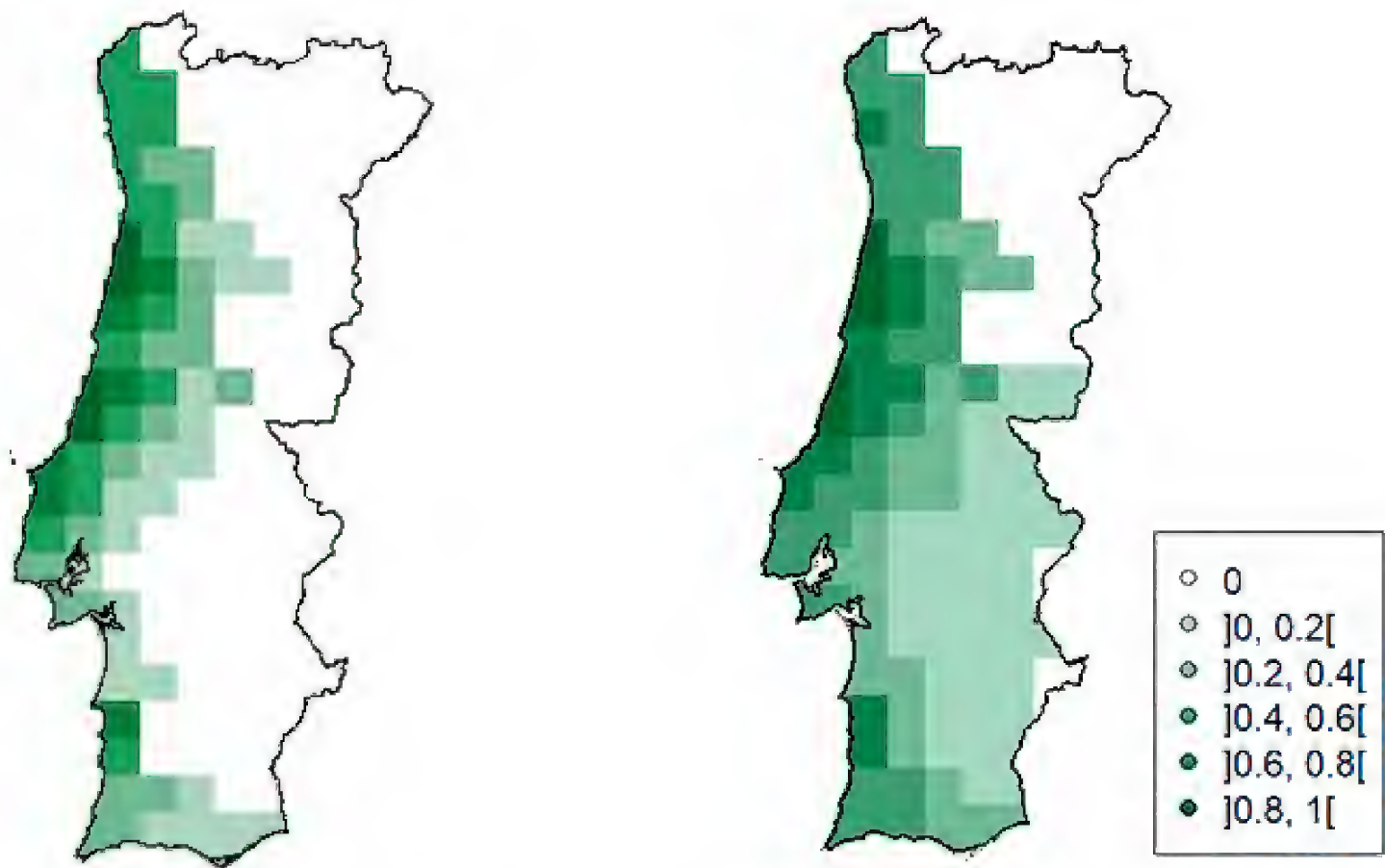
Figure 3. The estimated growth index of *Trioza erytreae* in Portugal, considering two fecundity levels: 327 eggs per female (left); 827 eggs per female (right).

Model validation

The model simulations that included long-distance dispersal fit the observed data better than those that did not (Table 3; see Suppl. material 1: tables S2 for *p*-values). This is shown by the significantly higher *F*1-Score between every model with the same combination of parameters besides the long-distance dispersal, independently of the frequency considered, i.e. low, medium or high (e.g. model 6 *F*1-Score = 0.733 vs. model 30 *F*1-Score = 0.803, *p*-value < 0.001; Table 3, see Suppl. material 1: table S2.1). The difference is even greater if the second introduction scenario is not considered (e.g. model 5 *F*1-Score = 0.583 vs. model 29 *F*1-Score = 0.801, *p*-value < 0.001; Table 3, see Suppl. material 1: table S2.1).

Different frequencies of long-distance dispersal events (low, medium and high) were not consistent in model improvement in all parameter combinations (Table 3, see Suppl. material 1: table S2.2).

The inclusion of the estimated urban and peri-urban citrus trees significantly increased the model performance, with significantly higher *F*1-score values in every model combination (e.g. model 30 *F*1-Score = 0.803 vs. model 32 *F*1-Score = 0.686, *p*-value < 0.001; Table 3, see Suppl. material 1: table S2.3).

The scenario of considering a second introduction was beneficial only for the simulations not using long-distance dispersal, when compared with similar models (e.g. model 6 *F*1-Score = 0.733 vs. model 5 *F*1-Score 0.583, *p*-value < 0.001; Table 3,

Table 3. The 32 different model simulations covering all parameter combinations and the corresponding *F*1-Scores for the model validation against the 2021 observed data.

Simulations	Parameters				Statistics	
	LDD	Fecundity	Urban trees	Second introduction	*F1*-Score	SE
1	No	low	Yes	No	0.530	0.0
2	No	low	Yes	Yes	0.669	0.0
3	No	low	No	No	0.421	0.0
4	No	low	No	Yes	0.546	0.0
5	No	High	Yes	No	0.583	0.0
6	No	High	Yes	Yes	0.733	0.0
7	No	High	No	No	0.463	0.0
8	No	High	No	Yes	0.596	0.0
9	low	low	Yes	No	0.791	0.0035
10	low	low	Yes	Yes	0.790	0.0029
11	low	low	No	No	0.640	0.0055
12	low	low	No	Yes	0.640	0.0060
13	low	High	Yes	No	0.804	0.0023
14	low	High	Yes	Yes	0.795	0.0023
15	low	High	No	No	0.689	0.0026
16	low	High	No	Yes	0.688	0.0024
17	medium	low	Yes	No	0.786	0.0043
18	medium	low	Yes	Yes	0.794	0.0036
19	medium	low	No	No	0.622	0.0065
20	medium	low	No	Yes	0.643	0.0053
21	medium	High	Yes	No	0.800	0.0024
22	medium	High	Yes	Yes	0.800	0.0024
23	medium	High	No	No	0.687	0.0021
24	medium	High	No	Yes	0.684	0.0021
25	High	low	Yes	No	0.789	0.0037
26	High	low	Yes	Yes	0.794	0.0027
27	High	low	No	No	0.615	0.0090
28	High	low	No	Yes	0.637	0.0058
29	High	High	Yes	No	0.801	0.0024
30	High	High	Yes	Yes	0.803	0.0023
31	High	High	No	No	0.683	0.0026
32	High	High	No	Yes	0.686	0.0018

see Suppl. material 1: table S2.4). The same was not true for model simulations considering long-distance dispersal. The parameter was sometimes not significant (e.g. model 9 *F*1-Score = 0.791 vs. model 10 *F*1-Score = 0.790, *p*-value = 0.97), sometimes beneficial (e.g. model 19 *F*1-Score = 0.622 vs. model 20 *F*1-Score = 0.643, p-value = 0.011) and sometimes negative towards model performance (e.g. model 13 *F*1-Score = 0.804 vs. model 14 F1-Score = 0.795, *p*-value = 0.006; Table 3, see Suppl. material 1: table S2.4).

Finally, model simulations that considered high fecundity (827 eggs per female) performed better those with low fecundity (327 eggs per female) in 6 out of 8 parameter combinations. In two cases, changing fecundity did not significantly affect

model performance (e.g. model 22 *F*1-Score = 0.800 vs. model 18 *F*1-Score = 0.794, *p*-value = 0.126; Table 3, see Suppl. material 1: table S2.5).

Overall, the model simulations with the highest performance were 13, 21, 22 and 30, showing no significant differences (see Suppl. material 1: table S2.6). All these models used long-distance dispersal, high female fecundity and urban citrus trees, but differed in the long-distance dispersal frequency and in considering the second introduction of *T. erytreae*.

Altogether and considering the temporal evolution between 2015 and 2021, our best model simulations showed a high concordance between the observed and predicted distribution of *T. erytreae* over the seven years after its detection in Portugal (Fig. 5).

Discussion

The major result of this study is that human-mediated dispersal and citrus trees outside orchards play an important role in the spread of *T. erytreae* in Portugal. Hereafter, we discuss in more detail these results as well as other findings.

Role of human-mediated dispersal

Human-mediated dispersal is a well-known documented phenomenon, recognised as a key issue in invasion science (Ricciardi et al. 2017; Bullock et al. 2018; Gippet et al. 2019). Human activities leading to insect dispersal can be divided into three pathways: Contamination, hitchhiking and harvesting (Pergl et al. 2017; Gippet et al. 2019). For the spread of *T. erytreae*, we believe the major pathways behind human-mediated dispersal of the species would be hitchhiking, as suggested for the invasion of *D. citri* in southern California (Bayles et al. 2017) and the invasion of the yellow-legged wasp, *Vespa velutina* in Portugal (Verdasca et al. 2021). In this pathway, adults' psyllids would be accidentally attached to a vehicle vector, from where they may be transported further away from their flight capacity, increasing the potential dispersal capacity of the species. This dispersal pattern coincides with higher dispersal along the coastline, where the human population is denser. It also reflects the distribution of north-south highways along the coast. Additionally, the movement of infested citrus plants is another possible pathway for the dispersal of *T. erytreae* in Portugal.

Since its detection, in 2015, the African citrus psyllid was able to spread mostly southwards, along the coastal area of Portugal, covering a maximum distance of about 461 km, between Porto and western Algarve, in seven years, corresponding to an average of about 66 km/year. This dispersal rate is about 4 to 8 times higher than the values reported for other Hemiptera, such as the hemlock woolly adelgid, *Adelges tsugae* Annand (Adelgidae) (8–13 km/year) and the beech scale, *Cryptococcus fagisuga* Lindinger (Eriococcidae) (14–15 km/year) (Liebhold and Tobin 2008). However, without considering long-distance dispersion events, the observed mean dispersal rate of *T. erytreae*

in Portugal was 7.8 km/year, similar to the spread rate of the other insect cases (Liebhold and Tobin 2008).

These results highlight that the spread of *T. erytreae* corresponds to a combination of short-range and occasional long-range dispersal events. This dispersal pattern, called "stratified dispersal" is commonly observed in the spread of invasive insect species (Liebhold and Tobin 2008). For *T. erytreae*, the inclusion of long-distance dispersal events greatly improved model performance in predicting the observed data (Table 3). In the current study, the large difference between the mean global dispersal rate (66 km/year) and the mean diffusion dispersal rate, estimated excluding the long-distance dispersal events (7.8 km/year), greatly highlights the importance of long-distance dispersal events for the species spread, which often are anthropogenic (Liebhold and Tobin 2008).

Likewise, the predicted and observed spread of *T. erytreae* along the coastal area of Portugal is also related with the high population density in the area, mostly between Porto and Setubal regions (Fig. 1), where long-distance dispersal events were concentrated. The role of human mediated dispersal was also reported in the yellow-legged hornet's rapid expansion along the coast of Portugal, attributed to the density of motorways (Verdasca et al. 2021). Nevertheless, motorways density and vehicle traffic are correlated with population density (Barata 2012). Although human-mediated movement of insect life stages is usually the dominant modality of long-distance dispersal, other mechanisms may also be involved, such as the wind, which has not been considered here. For example, Antolínez et al. (2022) showed that the dispersal of the Asian citrus psyllid, *D. citri* may be influenced by wind speed. On the contrary, wind direction was not found to be a significant factor in an experimental trial on *D. citri* dispersal conducted by Lewis-Rosenblumet et al. (2015). Nevertheless, Bayles et al. (2017) suggested that the observed spread pattern of the psyllid in California could be related with the prevailing wind direction, but without supporting a definitive conclusion. Future studies should investigate the possibility of assisted dispersal of psyllids in the upper wind, as an additional long-distance dispersal mechanism.

Our model provided contrasting results regarding the hypothesis of additional introductions of *T. erytreae* in Portugal during its invasion, as suggested by Ruíz-Rivero et al. (2021), based on the genetic diversity of *T. erytreae* populations. When not using long-distance dispersal in the model, including a second introduction, improved model performance towards predicting *T. erytreae* spread in Portugal (Table 3). Yet, when coupled with the long-distance dispersal parameter, the effect of a second introduction on model performance was inconsistent. This was shown by the best model simulations (13, 20, 21 and 30), that either used or did not use the second introduction parameter. This is likely due to long-distance dispersal diluting the importance of the introduction in the model since both have a similar impact on the model. In fact, the approach, which was used to include in the model an additional introduction of *T. erytreae*, was basically based on an input of individuals (1,000) in a defined cell of Lisbon area, which is not much different from a non-random long-distance dispersal event. This outcome further reveals that secondary introductions of invasive species

might be frequently misled with long-distance dispersals. Nevertheless, multiple introductions are more than just an addition of individuals to the founding invasive population. They may have an important role in incrementing genetic diversity of the invasive population, compensating the low genetic variability associated with founder effects (Handley et al. 2011). If this increment of genetic diversity is related with new adaptive traits, such as higher fecundity and/or survival rates, then additional introductions are expected to influence the dispersal dynamics of the invasive population. This scenario could be considered in the model, by changing the parameters fecundity and survival. In this respect, it is interesting to note that the higher fecundity value tested was associated with a higher performance of the model.

Role of urban and peri-urban citrus trees

Urban areas often facilitate the introduction, establishment and spread of non-native species, in biological invasions (Cadotte et al. 2017; Gaertner et al. 2017; Hui et al. 2017; Padayachee et al. 2017). Their green areas, including ornamental trees, public gardens, parks and backyard gardens, may function as stepping stones for non-natives species to disperse and invade agroecosystems (Hui et al. 2017). In Portugal, citrus trees are one of the most common plant species present in urban and peri-urban landscapes, used as ornamental plants in street trees, public gardens, parks, as well as food plants in backyard gardens. Using an innovative method, based on Google Street View imagery, we estimated the spatial distribution of those citrus trees outside orchards and its density according to Urban Areas typology (see Suppl. material 1: table S1). Our results showed that these citrus trees played a very important role in the dispersal of *T. erytreae* throughout the country (Table 3, see Suppl. material 1: table S2.3). For large areas of the observed distribution of the psyllid in 2021, where citrus orchards are almost non-existent (Fig. 2), the major source of host plants are the citrus trees in the urban and peri-urban areas (Fig. 4). This corroborates the previous claim that ornamental host species can contribute to connecting fragmented citrus-producing lands, as well as act as reservoir areas for the psyllid, especially in the framework of management actions in citrus-producing lands (Van den Berg et al. 1991).

Similarly, a recent study in California (Bayles et al. 2022), where citrus trees are also common ornamental and food plants in urban and peri-urban areas, also pointed out the importance that these trees played in the invasion dynamics of the Asian citrus psyllid, including its spill-over between urban and agricultural habitats (commercial citrus orchards).

Biological factors

We found no recent information in literature regarding female fecundity and no data available from Portugal on this parameter. For the modelling scenarios, we used two values provided in old literature, one considering a high fecundity of 827 eggs/female (Catling 1973) and an alternative one estimating a lower fecundity of 327 eggs/female (Moran and Blowers 1967) (Table 3, see Suppl. material 1: table S2.5). Our modelling results
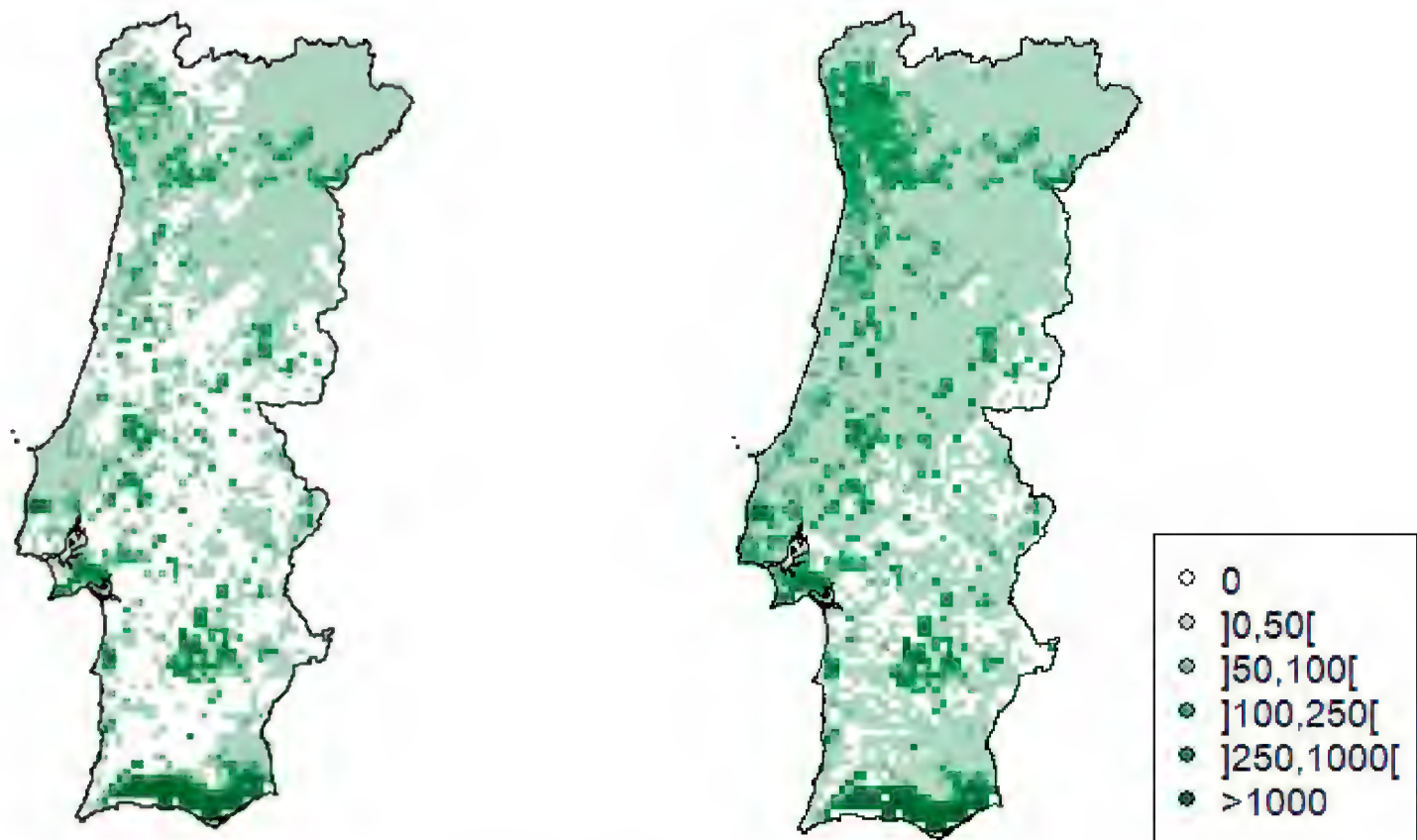
Figure 4. The spatial representations of the estimated citrus trees density (number of trees/km²) in Portugal. The left map represents the estimation of citrus trees density in Portugal, based on the area of citrus orchards reported in the last agricultural census (INE 2021), while the right map was obtained using both the data from the agricultural census (INE 2021) and our estimates of the number of citrus trees in urban and peri-urban areas, based on Google Street imagery.

showed significant differences according to this parameter, with the simulations using the higher fecundity performing significantly better than those with the lower fecundity. This outcome evidences the relevance to retrieve this type of basic biological data for the understanding of population invasion dynamics. Regrettably, these biological data are sometimes scarce and with low sampling power. Additionally, biological information may change with populations and differ in the invaded range. As these data are essential for modelling potential spread over several generations, we recommend that efforts should be spent on collecting such biological information on the invaded range of the species.

Model performance

Globally, our model was able to predict most of the spatio-temporal dynamics of *T. erytreae* spread quite well, except the recent invasion of the south-western area in 2021, in the coast of Alentejo and west coast of Algarve, for which the model predicted a low colonisation probability of 17% by the psyllid (Fig. 5). This low probability associated to a long-distance dispersal event, into the referred region, is explained by the low human population density in the region. However, a high seasonal touristic flow from the north occurring in this coastal area during Spring and Summer periods was not considered in our model. This large movement of people, including many residents from *T. erytreae*
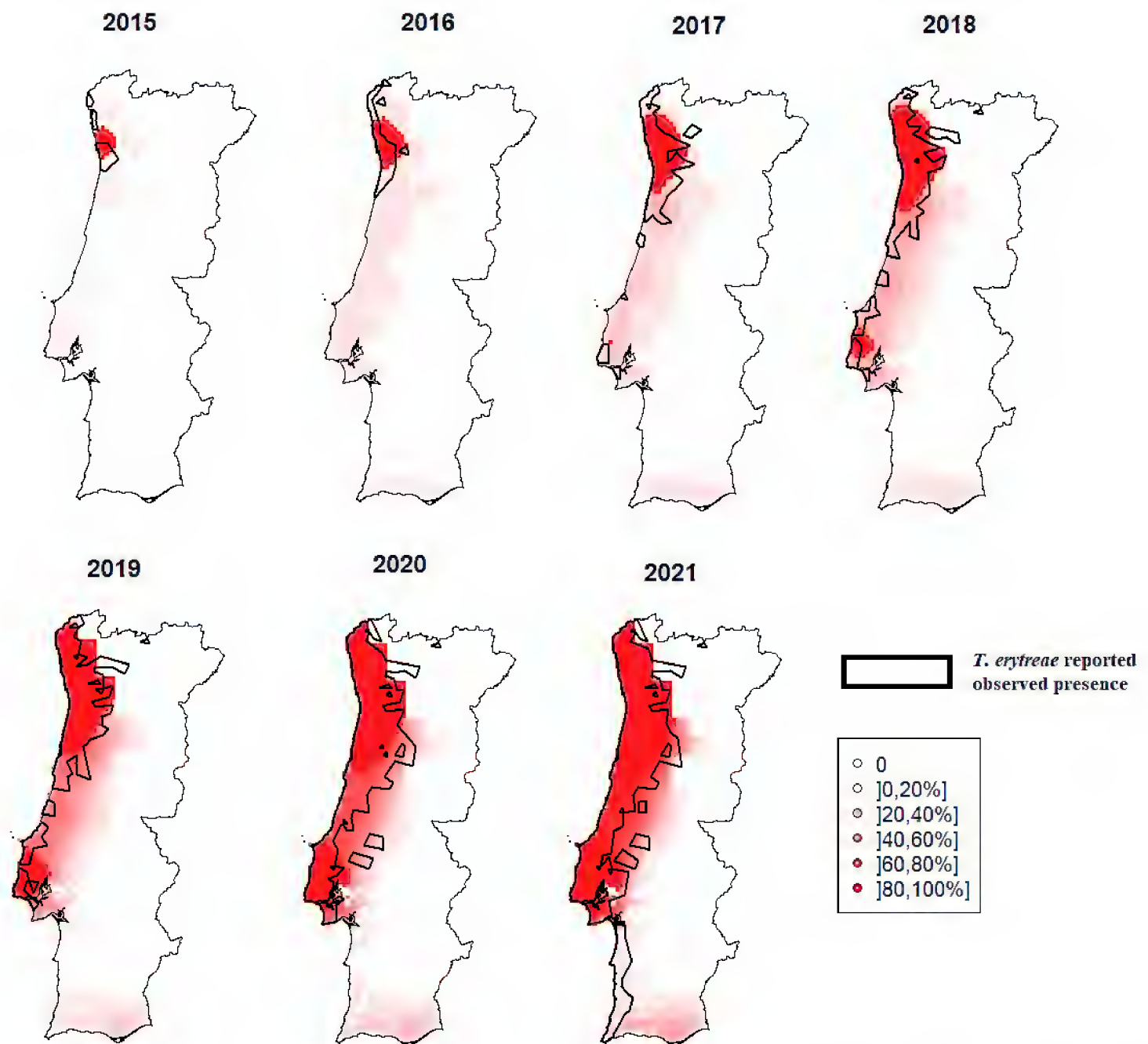
Figure 5. Spatio-temporal dynamics of *Trioza erytreae* spread in Portugal from 2015 up to 2021, predicted using 300 replicate simulations of model simulation #30. The colour gradient represents the probability of each grid cell to be infested according to the model, calculated as the relative number of simulations that predicted the area's infestation. The border of the observed distribution area of *T. erytreae* is represented by a black line (elaborated, based on data obtained from DGAV reports) to allow visual assessment of model performance.

infested areas, may favour hitchhiking mechanisms of dispersal (Gippet et al. 2019). Nevertheless, the observed presence of the psyllid in the area consisted mainly of small colonies or damage in isolated trees or small groups of trees in backyards and gardens (Amílcar Duarte, University of Algarve and Celestino Soares, DRAPALG pers. com., 2021). Furthermore, even if the model predicts low probability of invasion there, the probability is above 0, so it does not predict absence (Fig. 5). This infestation results from relatively rare and stochastic events, which are difficult to predict with a high probability.

The fast spread of *T. erytreae* in Portugal occurred despite the efforts carried out by the Portuguese Plant Protection Authority to contain its dispersal and eradicate it. The

measures implemented included the delimitation of demarcated areas, being the infested areas plus a buffer zone surrounding the infested areas with trap placement and active monitoring, along with various other control measures within the infested areas. Such control measures have not been accounted for in our spread model simulations and this may explain the reason why some areas in southern and inner Portugal, with relatively moderate predicted infestation probabilities, were not invaded by *T. erytreae* (Fig. 5). The apparent failure of the model in some parts of the country may result from a certain level of success of the implemented control measures.

Conclusions

Our model showed to be a good tool for simulating the invasion dynamics of *T. erytreae*. It was able to predict the observed spread of *T. erytreae* in Portugal from 2015 to 2021, when considering long-distance human-mediated dispersal and urban and peri-urban citrus trees. Our results support the hypothesis of human-mediated spread being a key-factor in the fast invasion of *T. erytreae* in Portuguese territory. This was highlighted by the fast spread pattern favouring the southern axis, mostly along the coastal area, where there is higher human population density, which was considered for the long-distance dispersal events in the model. Other factors possibly involved, such as the wind, should be considered in future studies. Our results did not support the hypothesis of a second invasion event of *T. erytreae* in Portugal. However, this hypothesis cannot be excluded, based on our results, since our model was not primarily designed to test the hypothesis.

Additionally, our work showed that citrus trees from urban and peri-urban environments had a very important role in the spread of *T. erytreae* in Portugal. This is highlighted by the major impact that they had on model performance, considering their very low relative number in comparison with the estimated orchard trees. Our results contribute to highlighting the importance that isolated host trees can have for species invasive dynamics. These trees are generally disregarded due to lack of statistical data. Finally, we showed that Google Street view imagery can be an efficient tool to estimate the density of urban and peri-urban trees.

Acknowledgements

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Supplementary material 1

Supplementary tables

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Data type: Docx file.

Explanation note: **table S1.** Estimated citrus tree density of each urban area class, the sampled area used for their estimation in hectares and the description of the urban and peri-urban area classes; **table S2.1.** p-values of the F1-score pair-comparisons between simulated models not using Long-distance dispersal (LDD) and model simulations using LDD with frequency ranging from low, medium and high; **table S2.2.** p-values of the F1-score pair-comparisons between simulated models using different Long-distance dispersal frequencies, low, medium and high; **table S2.3.** p-values of the F1-score pair-comparisons between simulated models using and not using the estimated urban citrus trees in the model; **table S2.4.** p-values of the F1-score pair-comparisons between simulated models with or without a second introduction of *Trioza erytreae* in 2017 in the model; **table S2.5.** p-values of the F1-score pair-comparisons between simulated models using *Trioza erytreae* higher or low female fecundity estimates (827 vs 327 eggs/female) for the model; **table S2.6.** p-values of the F1-score pair-comparisons between the best performing models, using F1-score as defining criteria.

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